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A New Rhynchosaur Taxon from the Popo Agie Formation, WY: Implications for a Northern Pangean Early-Late Triassic (Carnian) Fauna

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Abstract: New discoveries in the lower Popo Agie Formation (lower carbonate unit) of central Wyoming necessitated a reevaluation of USNM 494329 from the same unit, the only known hyperodapedontine rhynchosaur in western North America. Well known from Gondwanan deposits, hyperodapedontines appear to be restricted to the Carnian age (Late Triassic), with the exception of *Teyumbaita* in the earliest Norian age (Late Triassic) of Brazil. Initially assigned to c.f. '*Hyperodapedon*' *sanjuanensis*, our phylogenetic analyses reject this hypothesis, in support of a sister relationship between USNM 494329 (*Beesiiwo cooowuse*, gen. et. sp. nov.) and *Oryctorhynchus bairdi* forming an early-diverging clade that is only distantly related to '*H.*' *sanjuanensis*. Five additional specimens recovered from the lower Popo Agie are described. Three are referred to *B. cooowuse*, and another two are placed closer to *Hyperodapedon* and the remainder of Hyperodapedontinae. Our analysis demonstrates potential temporal distinction between a grade of earliest-diverging hyperodapedontines (including all Wyoming taxa) and a exclusively Late Carnian, Southern Pangaean hyperodapedontine clade (including '*H.*' *sanjuanensis*). We consider the lower Popo Agie Formation to represent the first nonmarine Late Triassic unit of Western North America that can be confidently restricted to the Carnian age.

Keywords: Popo Agie Formation; Late Triassic; rhynchosaur; Hyperodapedontinae; Carnian

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1. Introduction

The Late Triassic Carnian age (237–227 ma; [1]) is a critical interval in the diversification of many lineages that will play a prominent role throughout the Mesozoic (e.g., Mammaliaformes, Crocodylomorpha, Dinosauria; see [2] for review). However, fossiliferous terrestrial strata recording this age are largely absent in the Northern Hemisphere [3–5]. One of the clades that has limited representation in this region is Hyperodapedontinae (Rhynchosauria, Archosauromorpha), a group of stem-archosaurian reptiles that had a broad distribution across southern Pangaea throughout the Carnian and very earliest Norian (i.e., no younger than 225.4 Ma; [6–14]). Originally, *Otischalkia elderae* was described as a rhynchosaur from the Otis Chalk [15] and Bull Canyon Formation [16]; however, the general consensus concludes that these specimens belong to a non-rhynchosaur archosauromorph, most likely an azendohsaurid [10,12,17–19]. The only documented hyperodapedontines among northern Pangaen continents (North America, Eurasia) are the type species *Hyperodapedon gordoni* of the Lossiemouth Formation of Scotland [20,21], the fragmentary North American *Oryctorhynchus bairdi* from the Wolfville Formation of Nova Scotia [18], and

USNM 494329 (described as *Hyperodapedon* cf. *sanjuanensis*) from the Popo Agie Formation of Wyoming [22]. Since its initial description, USNM 494329 has been widely regarded to represent a distinct taxon (referred to as the "Wyoming *Hyperodapedon*" in [10]; and the "Wyoming form" in [13,18]). Phylogenetic analyses have repeatedly found USNM 494329 to be the sister taxon of *Oryctorhynchus bairdi*, demonstrating a previously unrecognized clade of North American rhynchosaurs [13,18]. However, this Popo Agie taxon has remained unnamed, and no additional material of this or other rhynchosaur taxa has been published from the Triassic of Wyoming since.

Here, we describe five new rhynchosaur specimens and redescribe USNM 494329; collectively, these specimens represent a significant and definite presence of rhynchosaurs in western North America during the early-Late Triassic. An assessment of the affinities of these and other North American rhynchosaurs reveals that all of the upper Chugwater elements are from hyperodapedontines. Three of these specimens represent a single novel taxa, *Beesiiwo cooowuse* gen. et sp. nov., which is sister to *Oryctorhynchus bairdi*.

2. Materials and Methods

2.1. Fossil Material and Imaging

While most surface texture and morphological features of specimens described herein have been lost or eroded beyond comparative use, the unique dental morphology of 12 new specimens allows for the referral of all to at least Rhynchosauria. A total of 5 of the 12 specimens contain enough morphological information to allow diagnosis to Hyperodapedontinae. The five undescribed specimens are all isolated maxillary tooth plates; BOR = TxVP 46037-1 and TxVP 46035-1; BLM = UWGM 7027, UWGM 7028, and UWGM 7029. A previously described specimen [22], USNM 494329 from Hole in the Wall, consists of a maxillary tooth plate, articulated dentary fragment, and an associated partial "premaxilla" (see Systematic Paleontology below).

UWGM 7027, 7028, and 7029 were µCT scanned at PaleoCT Scanner Facility at the University of Chicago with a General Electric Phoenix v | tome | x s 240 with a dual 180 tube. The scan parameters are as follows: 110 kV, 150 µA, 0.1 mm copper filter, 333 ms integration time, frame averaging of 3, 1 skipped frame, 1400 projections, scan time of 1 h: 3 min, and voxel size of 15.3150 µm.

2.2. Naming/Nomenclature Statement

The creation of new taxonomic names has a deep Western scientific tradition, complete with rules and regulations to maintain nomenclatural consistency and priority across languages and geopolitical borders (i.e., International Code for Zoological Nomenclature, Phylocode, etc.). While the rules and regulations are intended to codify a taxonomic lexicon used globally, taxonomic traditions are steeped in a history of colonization that is either unknown, unrecognized, or unacknowledged by most practitioners. We wish to acknowledge that the continued use of 'traditional' colonial practices, whether intentional or unintentional, is a biproduct of colonial history that needs be addressed. By way of example, names applied to new taxa that honor geographic features, regions, or waterways are often nomenclatural derivatives given by colonizers and do not reflect existing place names given by First Nations communities. Moreover, specific epithets are commonly bestowed upon specimens to honor colleagues or personalities both current and historical. Unfortunately, this traditional naming practice has led to an extraordinary disparity in representation perpetuating colonial practices and honoring the colonizer at the expense of First Nations peoples. Our collaborative team includes former and current officials of the Northern Arapaho Tribal Historic Preservation Office along with tribal Elders and linguistic experts. The taxonomic name *Beessiiwo cooowuse* was created by our Native co-authors in the Arapaho language to represent the type material collected on traditional and migratory lands of the Northern Arapaho. This name is intended to honor the Northern Arapaho people, their language, and their continued stewardship of the Earth.

2.3. Geological Setting

Late Triassic nonmarine continental strata of North America are limited to the Newark Supergroup (along the east coast) and the Chinle Formation, Dockum and Chugwater groups of the western United States (Figure 1). Relative to the Chinle and Dockum, comparatively little work has been done in the upper Chugwater Group of Wyoming, which includes the Popo Agie, 'unnamed red beds' (upper Crow Mountain), and Jelm formations. The Popo Agie Formation extends from west-central Wyoming through northeastern Utah [23,24]. It is the most fossiliferous unit of the relatively depauperate Chugwater Group and has been hypothesized to be early-Late Triassic in age based on vertebrate fauna [22,25–28].

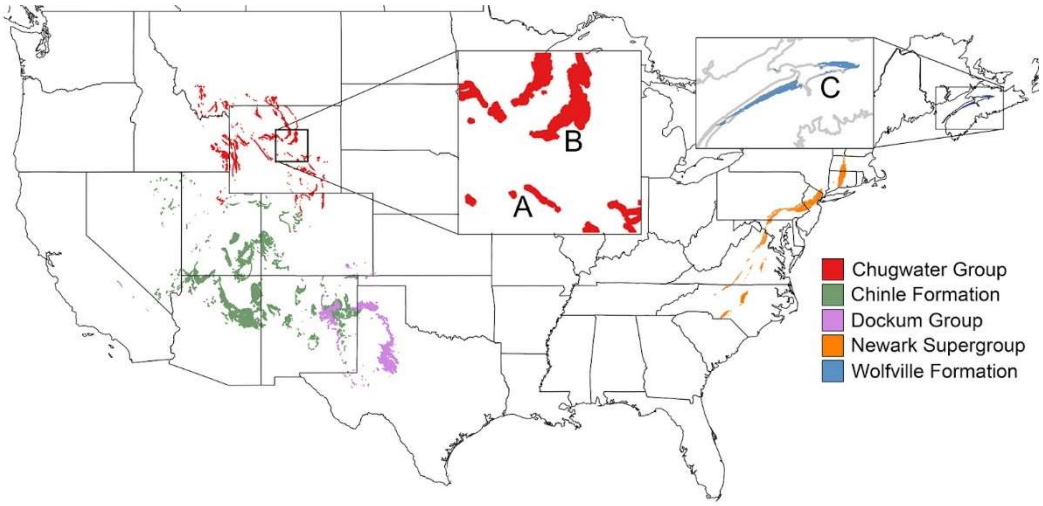

Figure 1. Exposures of continental Triassic strata across the contiguous United States and southern Canada. A = Cottonwood Creek (Alcova, WY); B = Hole in the Wall (Red Wall); C = Noels Head, Hants County, Nova Scotia [29].

Lucas [30] assigned an Anisian age to the lower Jelm based on the tentative identification of capitosauroid remains lacking morphological justification. Regardless of the validity of this identification, Capitosauroidea extends well beyond the Anisian, with definitive presence well into the Norian [31] rejecting the Anisian-age hypothesis. In light of this, few temporal constraints for the Jelm Formation of southeastern Wyoming exist (*sensu* [32]), although the upper Jelm (Sips Creek Member) has long been thought to be a lateral equivalent of the lower carbonate unit of the Popo Agie [23,24,32–35]. Although the spatiotemporal relationships between the type areas of the Popo Agie and Jelm formations remain largely qualitative, there is support for the equivalency of the upper Jelm in southern Wyoming and lower Popo Agie of central Wyoming. In west-central Wyoming, a stratigraphic unit given the unfortunate moniker 'unnamed red bed unit' (*sensu* [23]) has had a contentious nomenclatural and chronostratigraphic history. It has been defined as undifferentiated Jelm Formation [34,36] in west-central Wyoming, treated as an upper member of the Crow Mountain Formation [37] in central Wyoming, and even incorporated into the lowest unit of the Popo Agie [38]. Even though the 'unnamed red beds' have had an unstable place in the stratigraphic nomenclature, there is a consistent theme to all these descriptions and assignments: there is a prominent and widespread bone-bearing microconglomerate that can be traced over large distances.

The poor fossil record, and an absence of radioisotopic ages, chemostratigraphic or paleomagnetic constraints have also limited chrono- and biostratigraphic correlations of units within the upper Chugwater Group and Jelm Formation. In general, strata of the Chugwater Group thicken to the west towards the Idaho Trough, and thin to the east, typical of foreland basin geometry [35,39]. Gradual eastward truncation of upper Triassic strata by overlying Jurassic units is also well documented [35,40,41]. This is exemplified

by the progressive absence of analcime-rich portions of the upper Popo Agie that we have observed throughout southern and eastern Hot Springs County, disappearing just east of Bridger Creek, north of Lost Cabin, WY. The lower portion of the 'purple unit' of the Popo Agie—which lacks analcime typical of the upper Popo Agie [42,43]—remains observable in outcrop until central Red Wall where it is only intermittently present; the lower carbonate unit of the Popo Agie is consistently present below the purple unit and both units can be observed in outcrop as far south as Seminoe Reservoir, WY, and as far east as Hole in the Wall [40] (see Supplemental Data: Map).

There are several lithologies present in the lower Popo Agie that can be traced between sections within the eastern Wind River, southern Bighorn, and southwestern Powder River basins. Specifically, the presence of compositionally similar microconglomeratic lenses and channel forms that are coupled with a significant transition from arid to vertic floodplain paleosol characteristics typical of the lower carbonate and lower (non-analcime) purple units of the Popo Agie Formation [4,36,44–46]. These microconglomerates are dominantly composed of pebble-sized or smaller intraformational silt-rich to micritic carbonate clasts that lend the lower carbonate unit its name. These carbonate clasts are a common feature of outcrops of the basal Popo Agie Formation throughout western Wyoming where the continuity with overlying analcime-rich Purple and Ochre units are most apparent. We suggest lateral continuity exists between microconglomerates associated with overlying transitions to vertic paleosols throughout west-central and central Wyoming, and herein consider the localities at Hole in the Wall, and Cottonwood Creek to be within the lower carbonate unit of the Popo Agie.

2.4. Fossil Localities

2.4.1. Hole in the Wall

USNM 494329 was collected near the 'Hole in the Wall' area of the Red Wall, Southern Bighorn Mountains, WY (Figure 1). This collection area is 18 km north of the Clark Locality [47,48], where a silt-rich carbonate-dominated microconglomerate—ca. 10 m below the unconformable contact with Jurassic strata—forms the lower boundary of the *Heptasuchus* beds. The stratigraphic position of the USNM 494329 locality is reported in Lucas et al. [22], and although descriptions of lithologies and reasoning for the determination of formational boundaries were not presented, they demonstrated that USNM 494329 was found in a conglomerate ca. 15 m below the Triassic/Jurassic regional unconformity.

2.4.2. Cottonwood Creek

Near its outlet into Alcova Reservoir (Alcova, WY), Cottonwood Creek follows the contact between the dip slope of the Lower Triassic Alcova Limestone and overlying Upper Triassic strata [49,50]. The valley floor, when not covered by alluvium, expresses outcrops of what is locally identified as the Jelm Formation, though regionally it is considered Crow Mountain Formation [35,37,41,50]. The Cottonwood Beach Campground, managed by the Bureau of Reclamation (BOR), is built largely on floodplain and fluvial splay deposits, including locally expressed fossiliferous microconglomerates near the top of the section. Triassic-aged fossils have not previously been reported from Alcova Reservoir, although regionally, specimens of the Early Triassic pistosauroid *Corosaurus* are known from the late Spathian Alcova Limestone [50–52].

During the course of stratigraphic fieldwork in 2010, rounded bone elements were observed in microconglomerates along Cottonwood Creek, Alcova, WY. The microconglomerate is dominantly composed of silt-rich carbonate clasts and is physically traceable to equivalent beds on Bureau of Land Management (BLM) land a few hundred meters to the south. Twelve fragmentary specimens with rhynchosaur affinities, including 5 with diagnostic morphology (see Supplemental Data: Figure S1 for additional 7 specimens) were found as isolated clasts within microconglomeritic beds of the Cottonwood Creek area. Specimens were collected from BOR (Figure 2, localities 1-3; permit 11-GP-14-P) and BLM (permit PA09-WY-180) lands between 2011 and 2018. Other vertebrate fossil sites were

found in fine-grained fluvial sandstones immediately below the bone-bearing microconglomerate on BLM land. These sites produced a partial large archosaur quadrate, a small archosaur phalanx, and two vertebrae (UWGM 7030, 7034, 7035, and 1625, respectively; Supplemental Data: Figure S2) (Figure 2, locality 4).

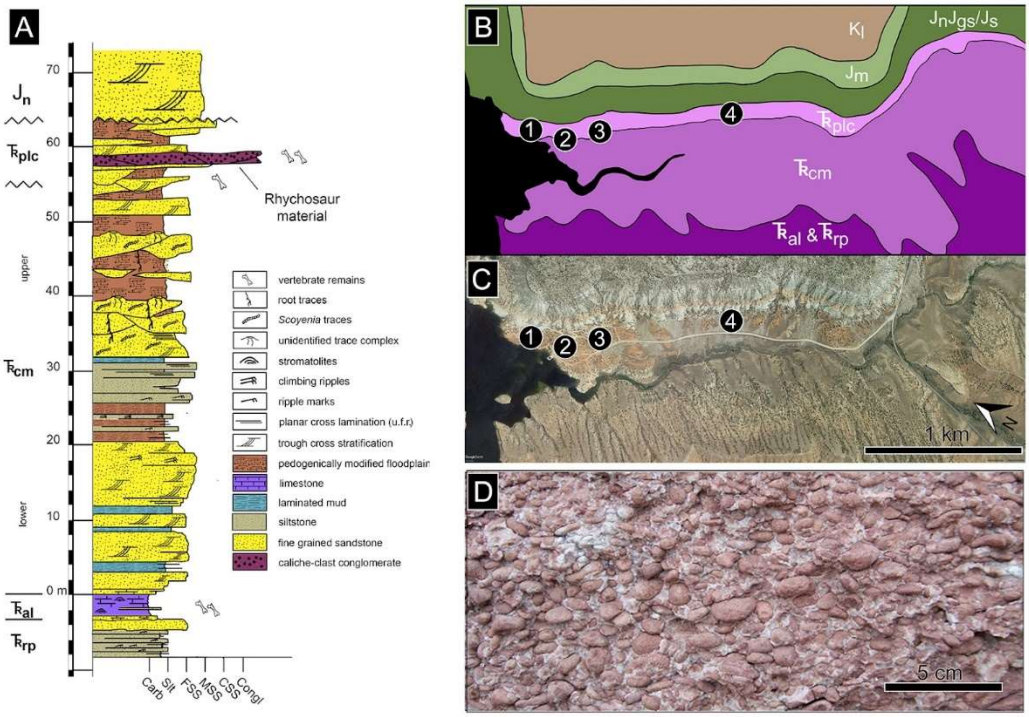

Figure 2. Stratigraphic profile (**A**) measured near Cottonwood Creek, Alcova, WY where four vertebrate localities (sites 1–4; **B**,**C**) yielded identifiable fossils discovered in a microconglomerate (**D**) several meters below the base of Early-Middle Jurassic strata. Red Peak Fm (Trrp); Alcova Limestone (Tral); Crow Mountain Fm (Trcm); lower carbonate of Popo Agie Fm (Trplc); Nugget (Jn); Gypsum Springs (Jgs); Sundance Fm (Js); Lakota Fm (Kl).

2.4.3. Stratigraphic Methods

The Cottonwood Creek section was measured with a Brunton Pocket Transit compass and Jacob's staff. Manual trenching was conducted where necessary to observe fresh, unweathered outcrop. A Munsell soil color chart was used to determine color of sediments, and a grain chart was used to quantify grain size. Copies of field notes are curated with the UWGM specimens listed below.

3. Results

3.1. Stratigraphy

We refer to the stratigraphic profile of Lucas et al. [22] for contextual information regarding USNM 494329. A stratigraphic section transecting the Cottonwood Creek Campground (Alcova) was measured to place the fossil-bearing beds into stratigraphic context. We consider the top of the Alcova Limestone to be a regionally correlative horizon [50] and use it to mark the base of the Cottonwood Creek stratigraphic section. Above the Alcova Limestone ca. 20 m of fine-grained trough cross stratified sandstone with interbedded laminated mudstones are typical of regional Upper Triassic strata (i.e., [32,37,41]). The next 10 m contain ca. 5 m of laterally extensive (100′s m scale) siltstone intervals interbedded with mudstone that demonstrates weakly developed peds, argillans, and rhizohaloes indicating minor pedogenic modification followed by 5 m of upper flow regime planar cross lamination siltstone to very fine-grained sandstone that we interpret to represent crevasse splay deposits (see [46]). The overall architecture of Upper Triassic strata at Alcova Reservoir is similar to that reported from the southern Bighorn Mountains [35,37,41]. Around

30 m above the contact with the Alcova Limestone there is a clear change in lithology. The following ca. 30 m are marked by 1–2 m thick lenticular fine-grained trough cross-stratified light-red (2.5YR 6/6) to pinkish-gray (7.5YR 7/2) sandstone bodies commonly incised into, and interbedded with, weak to moderately developed paleosols. The paleosols contain small blocky peds, argillans, and incipient to moderately developed Bk horizons with diffuse to well-formed micritic soil carbonate nodules; these paleosols are generally consistent with the inceptisol or aridisol families. Both the paleosols and the sandstone bodies contain abundant rhizoliths, rhyzohaloes and invertebrate traces dominated by adhesive meniscate burrows (AMB) [53,54]. In several sandstone lenses, a unique AMB-rhyzolith association forms discrete mounds elevated above the surrounding surface of the sandstone top (supplemental data: Figure S3). The remainder of the section (ca. 2–7 m) contains a locally expressed 0.5–2 m thick microconglomerate bed with prominent lateral accretion sets at its base. The microconglomerate is dominantly composed of well-rounded pebble-sized (1–2 cm diameter) silty-micritic carbonate clasts (Figure 2D). We interpret these to be intraformational clasts largely derived from Bk horizons in paleosols that host this bed. Those above the microconglomerate in the final 1–5 m of sediments are similar to those immediately below and are unconformably truncated by the overlying isolated eolian dunes of Jurassic-aged Nugget Sandstone or laminated shales of the Gypsum Springs Formation.

3.2. Age Assignment

We assign the bone-bearing microconglomerates of the Hole in the Wall and Alcova localities to the lower carbonate unit of the Popo Agie Formation, [22,36,47]. While there is no diagnostic parasuchid phytosaur fauna from the lower conglomerate of the Popo Agie Formation, all overlying layers of the Popo Agie exclusively contain non-leptosuchomorph parasuchids [27,55–61]. This restricts the overlying units to the Otischalkian Holochronozone *sensu* Martz and Parker [62]. The lower carbonate unit is thus older than the minimum termination age of the Otischalkian and initiation of the Adamanian holochronozones at roughly 221 Ma [62,63]. As such, in the absence of quantitative temporal constraints, we can only state that the lower carbonate unit (indeed, the Popo Agie as a whole) is no younger than pre-Adamanian. Considering the Spathian to earliest Anisian age of the Alcova Limestone ca. 60 m down section [50], the Hole in the Wall and Cottonwood Creek specimens are minimally constrained to somewhere between Anisian and early-Norian in age. Further work will be required to refine the temporal range of these strata (see argument below for restriction of units to the Carnian age of the Late Triassic).

3.3. Anatomic and Taxonomic Terminology

This paper follows Chaterjee [6] in referring to the successive maxillary tooth rows lateral to the groove dividing the maxillary tooth plate as LI, L2, L3, etc., respectively, and to those medial to this groove as Ml, M2, M3, etc., respectively, with L1 and M1 each positioned closest to the groove. Directional terms follow the standard nomenclature used in comparative vertebrate anatomy.

According to Article 23 of the International Code of Zoological Nomenclature (Fourth Edition; accessed 17 November 2022), the earliest given name for a taxon determinesnomenclatural priority, and according to PhyloCode Chapter V, Article 12 (Version 6; accessed 17 March 2023), converted clade name definitions are used so long as they are monophyletic and are the oldest phylogenetic definition for that taxon (though see final paragraph of this section). Respecting the priority of definition age and of phylogenetically defined clades, the oldest phylogenetic definition of Hyperodapedontinae (named in [64]), is found in the conversion of Langer and Schultz [7] as a branch-based taxon including all rhynchosaurid rhynchosaurs more closely related to the type species *Hyperodapedon gordoni* [21] than to the middle Triassic '*Rhynchosaurus*' *spenceri* ([65]; now the type species of the genus *Fodonyx sensu* [66]). The oldest definition fitting the aforementioned qualifications for the genus *Hyperodapedon* [21] is found in the conversion of the genus to a clade by Langer and Schultz [7], who define *Hyperodapedon* as a stem-based taxon consisting of all rhynchosaurs

closer to *Hyperodapedon gordoni* than to '*Scaphonyx*' *sulcognathus*. '*Scaphonyx*' *sulcognathus* has since been removed from the invalid genus *Scaphonyx* (whose type species is considered a *nomen dubium*, see below) and has been made the type species of the genus *Teyumbaita* [67]. Following the topology of Sues et al. [18], the only non-*H. gordoni* species of *Hyperodapedon* would be the Zimbabwean hyperodapedontine described by Raath et al. [68], which has yet to be formally taxonomically assessed at the generic/specific level. Following the topology of Langer et al. [13] and this work, no hyperodapedontine outside of *H. gordoni* can be included in *Hyperodapedon*. As such, following the topology recovered below, we consider the type genus and species of *Hyperodapedon*, *Hyperodapedon gordoni* [21], to be the only well-supported member of the genus at present. This leaves a significant number of taxa in need of generic placement; luckily, many genera have been proposed for various hyperodapedontine species prior to their subsequent inclusion within a speciose *Hyperodapedon*.

Before addressing valid genera, it is worth noting the myriads of genera which remain subsumed or otherwise not considered valid. We accept the junior synonymization of the genus *Stenometopon* with *Hyperodapedon* by Benton [20] as a result of junior synonymization of the type species of the former genus, *S. taylori*, with *H. gordoni*, also by Benton [20]; as such, we do not use *Stenometopon* further. The following hyperodapedontine genera are also not considered valid, as they were named with type species (in parentheses) that have since been considered *nomina dubia* [7,10,12,17,69–72]: *Scaphonyx* (*S. fischeri*; [73]), *Cephalonia* (*C. lotziana*; [74]), *Cephalastronius* (*C. augustispinatus*; [74]), *Cephalastron* (*C. gondwanicum*; [74]), and *Otischalkia* (*O. elderae*; [15]).

The remaining hyperodapedontine genera remain valid for use; these are *Macrocephalosaurus* ([75]; type species *M. mariensis*), *Paradapedon* ([76]; type species *P. huxleyi*), *Supradapedon* ([77]; type species *S. stockleyi*), *Isalorhynchus* ([78]; type species *I. genovefae*), *Teyumbaita* ([67]; type species *T. sulcognathus*), and *Oryctorhynchus* ([18]; type species *O. bairdi*). These genera account for the generic identity of all but three previously described hyperodapedontine species. Two of these previously described species, *Hyperodapedon huenei* [7] and *Hyperodapedon tikiensis* [10] were described as members of *Hyperodapedon*, while the remaining taxon, *Hyperodapedon sanjuanensis* [7,70], was initially described as a species of *Scaphonyx* before being subsumed into *Hyperodapedon* by [7]. As none of these three taxa share a sister relationship with *Hyperodapedon gordoni* to the exclusion of *Teyumbaita sulcognathus* ([13,18]; see below), and as a complete review of the taxonomy of the '*Hyperodapedon* complex' is beyond the scope of this paper, we will be referring to these species as '*Hyperodapedon*' *huenei*, '*Hyperodapedon*' *tikiensis*, and '*Scaphonyx*' *sanjuanensis*, respectively, in order to address their initial generic referral while acknowledging that their generic identity is unknown and in need of revision. Lastly, we follow [13] in using "the Zimbabwe form" to refer to an unnamed hyperodapedontine taxon from the Pebbly Arkose Formation of Zimbabwe described by [68].

This nomenclature aligns with the definition of priority given by the ICZN and the PhyloCode, with one exception found only in the latter. According to Chapter II, Article 4 of the PhyloCode (Version 6, accessed 17 March 2023), "distribution before the publication date of Phylonyms: A Companion to the PhyloCode of any material (printed or electronic) does not constitute publication". *Phylonyms: A Companion to the PhyloCode* was published 8 June 2020, and thus Langer and Schultz [7], published in 2000, is not considered officially published under the PhyloCode. As no phylogenetic definition of *Hyperodapedon* has been published following 8 June 2020, we strongly suggest that future revisions of hyperodapedontine taxonomy include a definition of *Hyperodapedon* equal to that of Langer and Schultz [7] for the following reasons: (1) under the ICZN, this definition has priority and this would allow for agreement between both systems, and (2) there is widespread use of the genus *Teyumbaita*, a genus currently deeply nested among hyperodapedontines, making potential future inclusion with the genus *Hyperodapedon* cumbersome.

4. Systematic Paleontology

Sauria McCartney, 1802 [79], *sensu* Gauthier et al., 1988 [80]

Archosauromorpha von Huene, 1946 [81] *sensu* Dilkes, 1998 [82]
Rhynchosauridae Cope, 1871 [83] *sensu* Dilkes, 1998 [82]
Hyperodapedontinae (Chatterjee, 1969 [64] nom. trans. ex Lydekker, 1885 [84] *sensu* Langer and Schultz, 2000 [7])

Beesiiwo gen. nov.

Etymology: *Beesiiwo*, from Arapaho "Beesiiwó" (pronounced " Bah - se - wa - ' ", with the apostrophe representing a glottal stop) meaning "big lizard".

Pronunciation guide: The sound for **b** is roughly as in English, but more like b before other consonants or at the end of a word; the sound for **ee** is as in the English 'bat' but is held longer; the sound for **s** is like in English, but always a nonvocailized, never vocalized as in some English s and all English z sounds; the sound for **ii** is as in English 'beat' but held longer; the sound for **o** is as in English 'hot; the sound for **'** is a glottal stop, as in the middle of oh-oh! in English [85]. See SI-Audio for recorded pronunciation, recording by ER.

Type Species: *Beesiiwo cooowuse* sp. nov., monotypic.

Diagnosis: As for type species, by monotypy.

Comments: The specimen NSM018GFF009.003, referred to *Oryctorhynchus bairdi* by Sues et al. [18], possesses two rows of lateral dentition and lacks posteriorly directed flanges on the L1 maxillary dentition, differing from the conditions of all other *O. bairdi* maxillae (which possess 1 lateral row and 1 medial row of maxillary dentition and possess posteriorly directed flanges on the L1 maxillary dentition). Beyond the possession of a crest-like maxillary tooth plate (shared with *Beesiiwo*), there is no unique support for this specimen as *Oryctorhynchus bairdi*, and we do not consider it a part of *O. bairdi*. These attributes better align with those found in *Beesiiwo cooowuse* (see below), and though it is beyond the scope of this work, we suggest it is either a close relative of this taxon or a member of such.

Beesiiwo cooowuse sp. nov.

Holotype: USNM 494329, fragment of a left maxilla and a left dentary.

Referred Specimens: UWGM 7027, fragment of a right maxilla; UWGM 7028, fragment of a right maxilla; TxVP 46037.1, fragment of a left maxilla.

Etymology: *cooowuse*, from Arapaho "co' oowu se'" (pronounced "ja' aw-wu sa'", with the apostrophe representing a glottal stop); meaning the "Alcova area", central WY.

Pronunciation guide: The sound for **c** is like that of the English j but without any puff of air and more like the English ch before other consonants or at the end of a word; the sound for **oo** is as in the English 'got' but held longer; the sound for **w** is like in English; the sound for **u** is as in the English 'put'; the sound for **e** is as in English 'bet' [85]. See SI-Audio for recorded pronunciation, recording by ER.

Occurrence: The type specimen was collected as clasts within a 0.5–1 m thick microconglomerate in the lower carbonate unit of the Popo Agie Formation near Hole in the Wall, Southern Bighorn Mountains, WY ('Willow Creek' of [22]). Referred material (see below) was collected as rounded to partially rounded clasts in a 0.5–2 m thick microconglomerate also referred to the lower carbonate unit of the Popo Agie Formation, Cottonwood Creek near Alcova, WY.

Diagnosis: Diagnosed by the following combination of character-states: maxilla with two lateral tooth rows and one medial tooth row; teeth of the lateral tooth row L1 lacking prominent anterolingual flanges; crest-shaped areas, respectively, medial and lateral to a longitudinal groove on the occlusal surface of the maxilla; dentary without a row of lingual teeth.

Description: "Premaxilla"—Lucas et al. [22] report a fragment of a premaxilla they believed to be paired with a maxilla and dentary, collectively identified as USNM 494329. We have reexamined this element and determined it is too fragmentary to be identified. As such, the premaxilla of *Beesiiwo cooowuse* is not currently known.

Maxilla—The maxilla of *Beesiiwo cooowuse* is represented by USNM 494329, UWGM 7027, TxVP 46037.1, and UWGM 7028. The maxillary tooth plate is a mediolaterally wide

occlusal surface that tapers anterodorsally toward the maxillary-premaxillary contact. The occlusal surface of all specimens is convex and exhibits medial and lateral maxillary crests that are separated by a prominent longitudinal groove. The cross-sectional shape of this groove becomes thinner and shallower towards its anterior termination. The presence of a longitudinal groove and of a convex occlusal surface are both synapomorphic of Rhynchosauridae [82,86]. This longitudinal groove extends well into the anterior half of the maxilla, as in most rhynchosaurids and unlike *Stenaulorhynchus stockleyi* and *Brasinorhynchus mariantensis* [12]. The lateral and medial portions of the maxilla, divided by the longitudinal groove, can be differentiated by the shape of the respective margin, concave in the former and convex in the latter. The longitudinal groove trends in the same direction as these margins, and so it can also be used to determine directionality when these faces are indiscernible. There is no medial maxillary groove similar to that found in *Fodonyx spenceri* [66], *'Hyperodapedon' huenei* [7], *Teyumbaita sulcognathus* [67], and the stenaulorhynchines *Brasinorhynchus mariantensis* [12], *Mesodapedon kuttyi* [77], and *Stenaulorhynchus stockleyi* [12,87]. The area lateral to the longitudinal groove is wider than the medial area, a trait uniquely found within Hyperodapedontinae, although it is absent in *Hyperodapedon gordoni* [20], *'Hyperodapedon' huenei* [7] and *Teyumbaita sulcognathus* [67]. The area lateral to the longitudinal groove is crest-shaped, as in *Isalorhynchus genovefae* [9,72], *Langeronyx brodiei* [17], *Oryctorhynchus bairdi* [18], *Teyumbaita sulcognathus* [67], and non-hyperodapedontine rhynchosaurids and unlike the cushion-shaped condition of some specimens of *Isalorhyncbus genovefae* and all other hyperodapedontines [72]. The area medial to the longitudinal groove is also crest-shaped, as in *Langeronyx brodiei* [17], *Oryctorhynchus bairdi* [18], *'Scaphonyx' sanjuanensis* [70], and *Paradapedon huxleyi* [6] and non-hyperodapedontine rhynchosaurids and unlike the cushion-shaped condition of all other hyperodapedontines [88].

Teeth are still partially present in all specimens, though they are weathered (syndepositional) to small prominences or to the level of the bone surface. Teeth irregularly vary from ellipsoidal to triangular or quadrangular in cross-section (Figures 3 and 4), the former of which are associated with a conical tooth shape and the latter a "pyramidal" tooth shape (both *sensu* [9]). The possession of both of these tooth morphologies is synapomorphic of Hyperodapedontinae [9], though only conical teeth are present in the potential hyperodapedontine *Langeronyx brodiei* [17]. All maxillary elements of *Beesiiwo cooowuse* possess multiple, anteroposteriorly arranged occlusal rows of ankylothecodont dentition diagnostic of rhynchosaurid rhynchosaurs [86]. None of the maxillae have teeth on the lingual surface, an absence shared with nearly all hyperodapedontines with the exception of *'Hyperodapedon' huenei* [7], *Langeronyx brodiei* [17], *Supradapedon stockleyi* [13], and *Teyumbaita sulcognathus* [67] and unlike the presence of such teeth in the aforementioned exceptions and in non-hyperodapedontine rhynchosaurids [89]. While the medial tooth rows are unknown in the holotype specimen USNM 494329, all referred maxillary material demonstrate that there is a single row (M1). The possession of a single medial row is only otherwise possessed by *Stenaulorhynchus stockleyi* [12,87] and *Rhynchosaurus articeps* [65], as all other rhynchosaurids possess two or more medial rows [9,13,18,89]. M1 lies tightly along the ventrolateral edge of the medial maxillary crest. The teeth in M1 are arranged with no interdental space and in such a fashion that their posterior surfaces face slightly posteromedially, leaving the maximum diameter of the tooth angled along (rather than perpendicular to) the longitudinal groove.

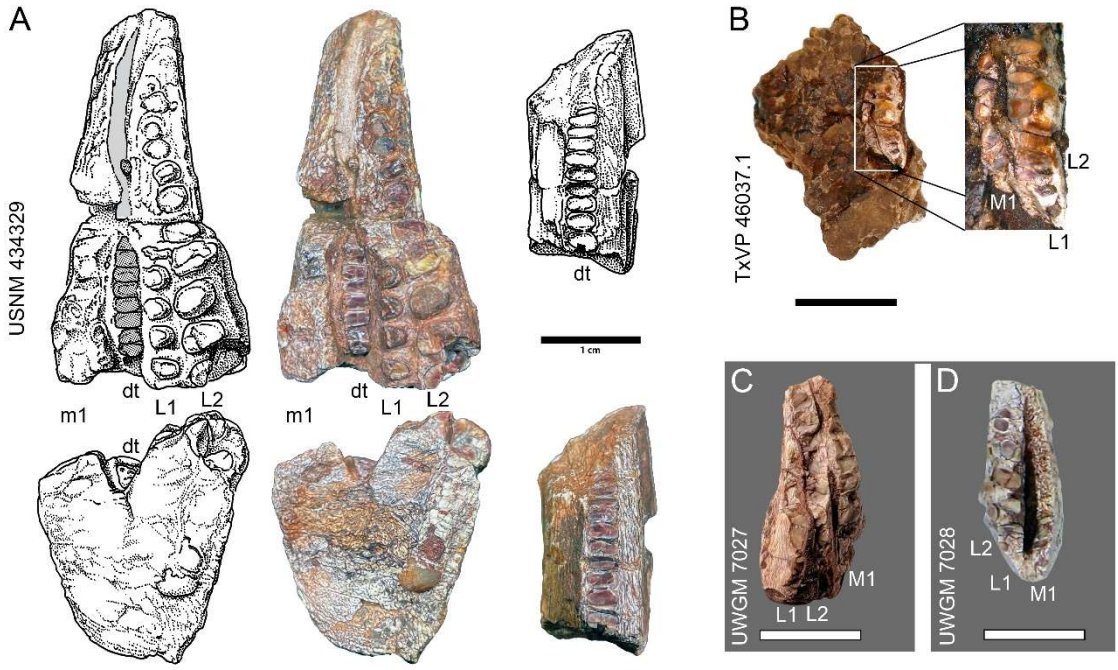

Figure 3. (**A**) The type specimen for *Beesiiwo cooowuse* (USNM 494329); occlusal view (top left/center) and axial cross section (bottom left/center) of posterior maxilla, and occlusal view of dentary (top/bottom right). Note that the row of teeth medial to L1 and L2 is not M1, but a fragment of the dentary that remains slotted into the longitudinal groove of the maxilla. (**B**–**D**) Occlusal view of three left maxillae from Cottonwood Creek referred to *Beesiiwo cooowuse*. Note the presence of M1 and absence of any additional medial rows. All scale bars = 1 cm. Illustration CC by Jim Morrison.

Figure 4. Hyperodapedontinae *indet.* Isolated maxillae (**A**) labial or lingual view (top left), occlusal view (right), and labial or lingual view (bottom left) of isolated partial maxilla TMM 46035.1. (**B**) occlusal view (top), labial or lingual view (bottom left), section through occlusal surface in occlusal view (upper left), and transverse section (bottom right) isolated partial maxilla UWGM 7029. Scale bars = 1 cm.

All maxillary specimens possess two lateral tooth rows; the possession of more than a single lateral tooth row is also present in *Mesodapedon kuttyi* [77] and nearly all of Hyperodapedontinae [7], though only one row is present in the early-diverging *Langeronyx brodiei* [17]. The teeth in L1 and L2 are larger than those in the medial row, as in *Oryctorhynchus bairdi* [18], *Isalorhynchus genovefae* [9], *Paradapedon huxleyi* [6], and *Langeronyx brodiei* [17] and unlike all other rhynchosaurids [17]. The lateral row dentition is also more irregular in size and orientation than are the medial teeth. The teeth in L1 and L2 are arranged in a staggered offset pattern, such that L1 is laterally bordered by L2. L1 rests on the ventromedial edge of the lateral maxillary crest, opposite M1. The maximum coronal

diameter of each L1 tooth lies roughly perpendicular to the longitudinal groove. L1 dentition lacks prominent anterolingual flanges, notably differing from *O. bairdi* [18]. Unlike in M1, there is interstitial space between each tooth in L1, in which the L2 teeth partially rest. L2 shows a similar morphology and size to L1, paralleling the longitudinal groove lateral to the L1 row in a staggered offset pattern until the anterior termination of L1, at which point the L2 row trends anteromedially until its termination along the longitudinal groove.

As a result of this dental morphology, the anterior half of the maxilla possesses less than four rows of occlusal dentition, as in *Isalorhynchus genovefae* [9], *Langeronyx brodiei* [17], *Oryctorhynchus bairdi* [18], and nearly all non-hyperodapedontine rhynchosaurids and unlike *Howesia browni* [90] and all other hyperodapedontines [9]. Additionally, more lateral rows are present than medial rows; the presence of a lateral row:medial row ratio of one or greater is also present in all hyperodapedontines with the exception of *Isalorhynchus genovefae* [9], *Langeronyx brodiei* [17], and *Supradapedon stockleyi* [17].

Some rhynchosaur taxa appear to have added rows of dentition throughout their ontogeny [88], potentially complicating the distinction of the aforementioned features. However, the maxillae representing *Beesiiwo cooowuse* cover a wide range of sizes, and yet all possess the same number of tooth rows (see Figure 3), a pattern also seen in *Isalorhynchus genovefae* [72,88] and in *Oryctorhynchus bairdi* [18]. As such, we believe that the aforementioned details of dentition reflect taxonomically valuable information and cannot be dismissed as of ontogenetic origin.

Dentary—A fragment of the left dentary in USNM 494329 represents the only mandibular material known from *Beesiiwo cooowuse*. The occlusion of the dentary with the maxilla is in a "blade and grove" fashion as a result of the dentary slotting into the longitudinal groove of the maxillary plate, synapomorphic of Rhynchosauridae [13,86]. There is only one row of occlusal dentary teeth and lingual teeth are absent; this condition is only otherwise found within Rhynchosauridae in *Oryctorhynchus bairdi* [18] and *'Scaphonyx' sanjuanensis* [22,70]. The teeth forming the occlusal row are mediodistally appressed such that there is no dental interstitial space and the teeth possess flattened mesial and distal surfaces, producing a subrectangular cross-section to the crown. This arrangement of dentary tooth crown morphology is unique to Hyperodapedontinae [9].

Sauria McCartney, 1802 [79], *sensu* Gauthier et. al., 1988 [80]

Archosauromorpha von Huene, 1946 [81] *sensu* Dilkes, 1998 [82]

Rhynchosauridae Cope, 1871 [83] *sensu* Dilkes, 1998 [82]

Hyperodapedontinae (Chatterjee, 1969 [64] nom. trans. ex Lydekker, 1885 [84] *sensu* Langer and Schultz, 2000 [7])

Gen. et sp. indet.

Materials: TxVP 46035.1, a fragment of a maxilla.

Occurrence: The specimen was collected as rounded to partially rounded clasts in a 0.5–2 m thick microconglomerate referred to the lower carbonate unit of the Popo Agie Formation, near Cottonwood Creek, Alcova, WY (see Figure 2).

Description: TxVP 46035.1 differs from *Beesiiwo cooowuse* in preserving at least two medial and two lingual rows that mirror one another in appearance across the longitudinal groove. The areas medial and lateral to the longitudinal groove are both, respectively, cushion-shaped in TxVP 46035.1 as in most hyperodapedontines with the notable exception of the crest-shaped condition of *Beesiiwo cooowuse* (see the description of *Beesiiwo cooowuse* for other exceptions; [12,88]). The lack of medial and lateral faces in addition to the poorly preserved longitudinal groove of TxVP 46035.1 makes it difficult to interpret many features typical of rhynchosaur maxilla. All teeth are arranged with roughly equal interstitial spacing, unlike the tightly aligned M1 row found in *Beesiiwo cooowuse*. M1 and L1 in TxVP 46035.1 possess teeth of varying-size and of both conical and "pyramidal" shape as demonstrated by their ellipsoidal or angular/sub-triangular occlusal cross sections; the presence of both tooth shapes is unique to Hyperodapedontinae [9]. As in L1 of *Beesiiwo cooowuse*, ellipsoidal teeth in M1 and L1 are arranged with a mediolaterally trending

maximum coronal diameter. M2 and L2 are very poorly preserved in TxVP 46035.1, with only 2 preserved teeth in each row, in addition to one medial most surface of analveolus that is visible in cross-section. The remnants of this row possess circular occlusal cross sections and are within the size range of the M1 and L1 teeth, suggesting that all preserved rows were likely similar in general morphology. As with *Beesiiwo cooowuse*, the possession of more than a single lateral tooth row is shared with *Mesodapedon kuttyi* [77] and is otherwise unique to Hyperodapedontinae [7]. Dentition on either side of the groove is subequal in size, meaning that the lateral dentition is subequal to the medial dentition as in most rhynchosaurids, with the notable exception of *Beesiiwo cooowuse* (see description above for other exceptions; [13]).

Sauria McCartney, 1802 [79], *sensu* Gauthier et. al., 1988 [80]

Archosauromorpha von Huene, 1946 [81] *sensu* Dilkes, 1998 [82]

Rhynchosauridae Cope, 1871 [83] *sensu* Dilkes, 1998 [82]

Hyperodapedontinae (Chatterjee, 1969 [64] nom. trans. ex Lydekker, 1885 [84] *sensu* Langer and Schultz, 2000 [7])

Materials: UWGM 7029, a fragment of a left maxilla.

Occurrence: UWGM 7029 was collected ex situ as a broken, partially rounded element on an upper exposure surface of a 0.5–2 m thick microconglomerate referred to the lower carbonate unit of the Popo Agie Formation, near Cottonwood Creek, Alcova, WY (see Figure 2).

Description: UWGM 7029 is unique among Chugwater rhynchosaur remains and preserves five rows of near homogenous dental row composition. The area medial to the longitudinal groove is cushion-shaped, as in TxVP 46035.1 and most hyperodapedontines and unlike the crest-shaped condition of *Beesiiwo cooowuse* (see description of *Beesiiwo cooowuse* above; [12]); the shape of the area lateral to the longitudinal groove cannot be interpreted due to extensive damage and absence of the lateral aspects of the area in the specimen. As in TxVP 46035.1, teeth on either side of the groove are subequal in size, as in most rhynchosaurids with the notable exception of *Beesiiwo cooowuse* (see *Beesiiwo cooowuse* description above for other exceptions; [13]). A minimum of two dental rows are preserved on either side of the longitudinal groove; the second row of dentition is exposed as a sagittal cross section along an anteroposterior break and it is unknown if more than two rows existed. As with all of the material described above, the presence of multiple lateral rows is shared with *Mesodapedon kuttyi* [77] and all of Hyperodapedontinae with the exception of *Langeronyx brodiei* [17]. On the opposite side of the longitudinal groove, three distinct rows are present. Teeth in UWGM 7029 are arranged with roughly equal interstitial spacing and vary from ellipsoidal to triangular or quadrangular in horizontal cross-section (Fig 4B), the former of which is associated with a conical tooth shape and the latter a "pyramidal" tooth shape *sensu* [9]. As previously mentioned, the presence of both conical and "pyramidal" tooth morphologies is unique to Hyperodapedontinae [9].

Phylogenetic Relationships

To assess the affinities of this collection of non-associated specimens, *Beesiiwo cooowuse*, TxVP 46035.1, and UWGM 7029 were scored in the character-taxon matrix of [13] with the addition of *Oryctorhynchus bairdi* to the matrix by [18], bringing the matrix to 27 OTUs (see supplemental data SI-NEX and SI-TNT).

Some changes were made to preexisting characters and codings. Character state 1, "more than one clear row", of character 69 (addressing the number of maxillary lateral tooth rows) was split from into states 1, 2, 3, and 4, which, respectively, represent two, three, four, and five or more rows of lateral dentition, and the character was made ordered as a result. Character 70, addressing the number of medial tooth rows, is already ordered, and its state 2, "three or more tooth rows", that was split into states 2, 3, and 4, respectively representing three, four, and five or more rows of medial dentition. Character state 1 of character 78 (concerning the presence of dentary lingual dentition) was split into character states 1, "present as single row", and 2, "present as two rows", and the character was made ordered

as a result. Character 79, addressing the number of rows of lingual dentition, is deactivated, as this is redundant with the altered states of character 78. Similarly, character 121, which addressed the relative proportions of the numbers of lateral and medial maxillary tooth rows, was deactivated as it is irrelevant given the coverage of character 69 (addressing the number of lateral maxillary tooth rows) and character 70 (addressing the number of medial rows). The character codings of *Bentonyx sidensis* were changed in the following characters, based on [91]: character 12 (1 -> 0), character 47 (1 -> ?), character 63 (1 -> ?). *Langeronyx brodiei* was recoded for character 12 (1 -> 0; [17,65]). The codings of *Oryctorhynchus bairdi* were changed for character 70 (1 -> 0&1; [18]).*Fodonyx spenceri* was recoded for character 122 (0 -> 1; [65]). Lastly, the codings of character 123 were changed for *Hyperodapedon gordoni* (0 -> 0&1; [20]) and the "Zimbabwe form" (0 to 0&1; [92]).

Additionally, three new characters were added to the dataset:

- 124. Lacrimal, contacts the ascending process of the palatine: (0) absent; (1) present.
- 125. Maxilla, occlusal view, labiolingual distance between longitudinal groove apex and L1 tooth row: (0) less than the labiolingual width of L1 teeth; (1) equal to or greater than the labiolingual width of L1 teeth.
- 126. Maxilla, ascending process: (0) anterodorsal–posteroventral orientation of contact with the prefrontal and/or lacrimal; (1) nearly vertical orientation of contact with the prefrontal and/or lacrimal.

Using the following references, all taxa were coded for these characters, as well as the necessary recodings of the reworked states of characters 69 and 70: *Ammorhynchus navajoi* [89], *Bentonyx sidensis* [66,91], *Brasinorhynchus mariantensis* [12], *Eohyosaurus wolvaardt* [11], *Fodonyx spenceri* [65,66], *Howesia browni* [90], *Hyperodapedon gordoni* [20], *'Hyperodapedon' huenei* [7], *'Hyperodapedon' tikiensis* [10], *Isalorhynchus genovefae* [9], *Langeronyx brodiei* [17,65], *Macrocephalosaurus mariensis* [13,93], *Mesodapedon kuttyi* [10,77], *Mesosuchus browni*), *Oryctorhynchus bairdi* [18], *Paradapedon huxleyi* [6], *Prolacerta browni* [94,95], *Protorosaurus speneri* [96], *Rhynchosaurus articeps* [65], *'Scaphonyx' sanjuanensis* [93,97], *Stenaulorhynchus stockleyi* [86,93], *Supradapedon stockleyi* [13], *Teyumbaita sulcognathus* [67], and the "Zimbabwe form" [68,93].

The data matrix was analyzed in TNT v. 1.5 [98,99]. An "Implicit Enumeration" analysis using "Collapse of Trees after Search" was run. *Protorosaurus speneri* was set as the primary outgroup, and characters 69, 70, 76 and 78 were treated as additive. All other parameters were left in their default settings.

This analysis resulted in 32 most parsimonious trees with a length of 235. The recovered trees had a consistency index of 0.574 and a retention index of 0.792. A strict (=Nelson) consensus tree was generated from these and found all three OTUs to represent hyperodapedontine rhynchosaurids (see Figure 5A for full topology, bremer support, and bootstrap values). *Beesiiwo cooowuse* is found to be the sister taxon to *Oryctorhynchus bairdi* based on the shared presence of a single medial row of maxillary teeth (char. 70, state 0), the presence of a single row of dentary teeth (char. 76, state 0), the absence of lingual dentary teeth (char. 78, state 0), and a crest-shaped maxillary plate cross-section medial to the primary longitudinal groove (char. 109, state 0). TxVP 46035.1 and UWGM 7029 are recovered in a polytomy with *Hyperodapedon gordoni*, *Paradapedon huxleyi*, the 'Zimbabwe form', and a clade containing the remaining hyperodapedontines (with the exception of *Isalorhynchus genovefae*, here the earliest diverging hyperodapedontine). This polytomy is supported based on the shared presence of a cushion-shaped area lateral to the main longitudinal groove (char. 68, state 1; present in TxVP 46035.1 but unknown in UWGM 7029), three or more lateral rows of maxillary occlusal teeth (char. 69, state 2, 3, 4; cannot be definitively shown as present in these but is present in *H. gordoni* and *P. huxleyi*), four or more rows of occlusal teeth in the anterior half of the maxilla (char. 71, state 0; same situation as char. 69), and a cushion-shaped area medial to the main longitudinal groove (char. 122, state 0; present in TxVP 46035.1 and UWGM 7029). The aforementioned clade within this polytomy is supported by a pterygoid midline suture length that is greater than or equal to the distance between the caudal margin of the suture and the basipterygoid articulation (char. 45, state 0) and a labiolingual distance between the occlusal apex of the

longitudinal groove and the lingual edge of the L1 dentition that is equal to or greater than the labiolingual diameter of the L1 dentition (char. 125, state 1), notably (and only) the latter of which is definitively absent in TxVP 46035.1 and UWGM 7029.

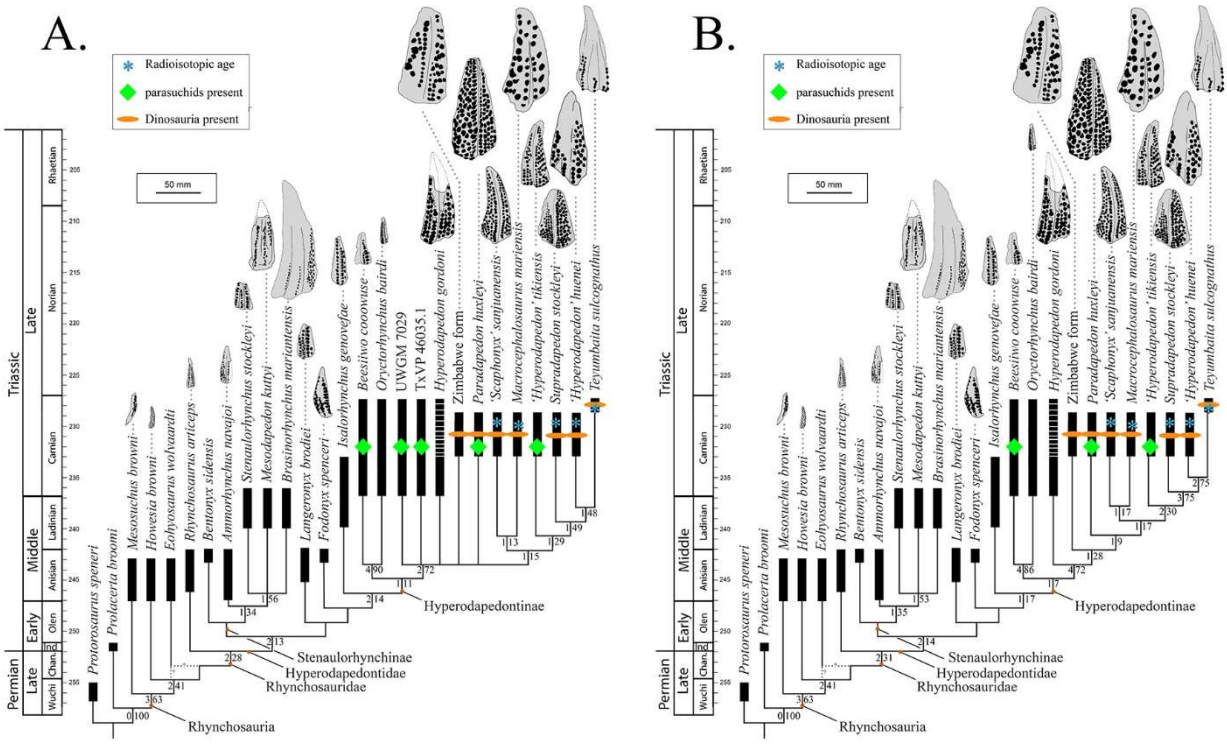

Figure 5. Strict consensus of 32 MPTs (length = 235). (**A**) Strict consensus of 32 MPTs (length = 235) with TxVP 46035.1 and UWGM 7029; (**B**) Strict consensus of 2 MPTs (length = 235) with the a priori removal of TxVP 46035.1 and UWGM 7029. Note the endemic North American clade formed by *Oryctorhynchus bairdi* and *Beesiiwo cooowuse* in both analyses and the polytomy between TxVP 46035.1and UWGM 7029 and a cosmopolitan assemblage of later-diverging hyperodapedontines in the first analysis.

In light of the polytomy, we reran the analysis with the a priori removal of TxVP 46035.1 and UWGM 7029. This revised analysis resulted in 2 most parsimonious trees with a length of 235. The recovered trees had a consistency index of 0.574 and a retention index of 0.792. A strict (=Nelson) consensus tree was generated from these and found the same topology as the first analysis, including the same relationship (and character support for such) between *Beesiiwo cooowuse* and *Oryctorhynchus bairdi*, with the exception of the absence of the aforementioned polytomy (see Figure 5B for full topology and node support values). This topology is rather similar to that of Sues et al. [18], with a few notable exceptions. *'Scaphonyx' sanjuanensis* is recovered for the first time as the sister taxon to *Macrocephalosaurus mariensis* based on the shared absence of lacrimal contact with the ascending process of the palatine (char. 124, state 1), unique to these among sampled taxa. Additionally, *Bentonyx sidensis* is recovered as the earliest diverging stenaulorhynchine, based on the shared presence of a markedly concave postfrontal dorsal surface (char. 28, state 1), a rounded depression on the ventral surface of the basisphenoid (char. 105, state 1), and a nearly vertical contact of the posterior surface of the maxillary ascending process with the prefrontal and/or lacrimal (char. 126, state 1). *Hyperodapedon gordoni* and the 'Zimbabwe form' do not have a sister taxon relationship here, with the 'Zimbabwe form' being closer to a clade consisting of *Teyumbaita* and most other hyperodapedontines (see topology below) based on the shared presence of more than three lateral rows of maxillary occlusal teeth (char. 69, state 3, 4).

5. Discussion

Beesiiwo cooowuse, TxVP 46035.1, and UWGM 7029, drastically expand our rhynchosaur diversity within North America and demonstrate the presence of both North American endemic and cosmopolitan hyperodapedontines in western North America. New material from the upper Chugwater Group of central Wyoming demonstrates a greater North American rhynchosaur diversity than was previously appreciated. We find support for an endemic North American clade (*Oryctorhynchus*+*Beesiiwo*) in addition to a contemporaneous presence of later-diverging members of a cosmopolitan clade within North America. The Popo Agie material represents the largest definitive record of rhynchosaurs in North America (see Figure 6 for life reconstruction).

Figure 6. Life reconstruction of *Beesiiwo cooowuse* with *Heptasuchus clarki* in the background representing the known fauna from the lower carbonate unit of the Popo Agie Formation. Copyright, Gabriel Ugueto.

Our support for a non-*Hyperodapedon* hyperodapedontine assignment for *Beesiiwo*, in addition to the specific restriction of the genus *Hyperodapedon* to only its type species (see above), brings into question the validity of using hyperodapedontine rhynchosaurs in vertebrate biostratigraphy. *Hyperodapedon* is the index taxon for the Carnian-equivalent *Hyperodapedon* biozone (*Hyperodapedon* Assemblage Zone, *sensu* [15,22]; *Hyperodapedon* ACME Zone, *sensu* [100]; *Hyperodapedon* biozone *sensu* [14]). While the *Hyperodapedon* of this biochron is now considered to be several genera (this work, [18,67,72]), there is little reason to think the presence of Hyperodapedontinae, which is equal in current taxonomic inclusion (see above), could not still be informative for both the Popo Agie Formation and units bearing this taxon worldwide. The oldest hyperodapedontine from southern Pangaea is *Isalorhynchus genovefae* from the lower Isalo II (Makay Formation; [9]). Material of *Isalorhynchus* has been found with material of the cynodont *Menadon besairei* [101], a taxon otherwise exclusively found within the *Santacruzodon* assemblage zone of the Santa Maria supersequence of Brazil ($\leq$237 $\pm$ 1.5 Ma; [102]). Conversely, hyperodapedontines have long been established to go extinct from southern Pangaean faunas at ca. 227 Ma (227.24 + 1.27/$-$ 1.97 Ma; [14]). Within northern Pangaea, hyperodapedontines are only found from three localities. The Lossiemouth Sandstone in Scotland preserves material of the hyperodapedontine *Hyperodapedon gordoni*, but the locality lacks absolute age estimates and is not currently placed within any of the aforementioned biochronozones nor any Atlantic rift basin tectonosequences (TS), and so its age remains uncertain. The TS II

(>228.5 Ma) Evangeline Member of the Fundy Basin contains the sole material of the hyperodapedontine *Oryctorhynchus bairdi* [18]. In western North American deposits, the only diagnostic hyperodapedontine material is from the Otischalkian lower carbonate unit of the Popo Agie Formation ([60], this paper). The chronostratigraphic distribution of hyperodapedontines within northern Pangaea is either in agreement with the Carnian-exclusive southern Pangaean hyperodapedontine range or is too poorly understood to contribute to or contradict this range. As such, all available evidence at presence supports the use of Hyperodapedontinae as a Carnian (ca. 237–227 Ma) index taxon. We consider the first appearance of Hyperodapedontinae to represent the initiation of the *Hyperodapedon* biozone and suggest its name be changed accordingly to the Hyperodapedontine biozone.

Furthermore, there appears to be additional potential for chronostratigraphic signal within Hyperodapedontinae, as well. All hyperodapedontine taxa recovered here as closer related to *Teyumbaita sulcognathus* than to *Hyperodapedon gordoni* cooccur with dinosaurs, while *Hyperodapedon gordoni* and all earlier diverging rhynchosaurs are exclusively found from units that do not possess dinosaurs (see list of references in 'Phylogenetic Relationships'; see [92]). Furthermore, of this latter group of rhynchosaurs, only four, *Isalorhynchus genovefae*, *Oryctorhynchus bairdi*, *Hyperodapedon gordoni*, and the lower carbonate Popo Agie hyperodapedontines do (*Isalorhynchus*) or are predicted to (*Oryctorhynchus*, *Hyperodapedon*, *Beesiiwo*) occur in the Late Triassic, with all non-hyperodapedontine rhynchosaurs being restricted to the Early and Middle Triassic (see [17]). Dinosaurs first appear in the upper Santa Maria Formation of Brazil (ca. 233.23 ± 0.73 Ma; [103]) and the Ischigualasto Formation of Argentina (see [14]) and are notably absent from the earlier Carnian *Massetognathus*-*Chanaresuchus* assemblage zone of the Agua de la Peña Group of Argentina and the equivalent *Dinodontosaurus* assemblage zone of the lower Santa Maria Formation of Brazil, as well as the aforementioned Isalo II units of Madagascar that produced *Isalorhynchus*. While the Lower Popo Agie fauna has always been somewhat fragmentary and is at present not the best test of dinosaur presence or absence, the Lossiemouth Sandstone has produced a diversity of Late Triassic tetrapods large and small and yet has never produced a dinosaur; its sole dinosauromorph is the diminutive non-dinosaurian dinosauriform *Saltopus elginensis* [104]. As such, we propose that Hyperodapedontinae consists of an earliest-diverging grade that originated prior to the appearance of dinosaurs (>ca. 233 Ma) and a later clade nested within this grade that occurs with them until the extinction of Hyperodapedontinae (and all Rhynchosauria) ca. 227 Ma. This would give the *Oryctorhynchus*-bearing Evangeline Member of the Wolfville Formation, the *Hyperodapedon*-bearing Lossiemouth Sandstone, and the lower carbonate unit of the Popo Agie Formation an age restriction of 237–233 Ma.

In light of the Carnian restriction of the basal unit of the Popo Agie, this supports that at least the lower carbonate unit of the Popo Agie Formation fills part of the Ladinian to early-Norian gap of terrestrial strata in North America. This ca. 20 million year gap in the rock record encompasses the entirety of the Ladinian, Carnian, and early Norian, a temporal span that extends beyond the last global occurrences of rhynchosaurs [4,14,67]. The otherwise apparent absence of hyperodapedontine rhynchosaurs across the continent is likely a result of this appreciable stratigraphic gap, indicating that the biogeographic restriction of Hyperdapedontinae is a preservational (i.e., not biogeographic) phenomenon. This too lends support to the use of Hyperodapedontinae as a key taxon for regional and global biostratigraphic correlations (as with its predecessors, e.g., *Hyperodapedon* Assemblage Zone, *sensu* [15] and *Hyperodapedon* ACME Zone, *sensu* [100]). Considering the near-absence of Carnian-aged terrestrial strata in the Northern Hemisphere, *Beesiiwo* and the Popo Agie rhynchosaurs supports the presence of an exceptional Carnian fauna preserved in the lower carbonate unit, if not the entire Popo Agie Formation.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15040544/s1, Map: Wyoming locations discussed in text; Figure S1: Additional rhynchosaur indet. material; Figure S2: Additional vertebrate material; Figure S3: Invertebrate traces; Audio S1: Pronunciation.

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Abbreviations

TxVP, Texas Vertebrate Paleontology Collection, Jackson Museum of Earth History at The University of Texas, Austin, TX USA; NSM, Nova Scotia Museum of Natural History, Halifax, NL, CA; USNM, Smithsonian National Museum of Natural History, Washington, DC, USA; UWGM, University of Wisconsin Geology Museum, Madison, WI, USA; PEFO, Petrified Forest National Park.

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